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THEORIES OF HIBERNATION

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An examination of the literature on almost any particular natural phenomenon often reveals the fact that many different theories have been advanced to explain it. Some of these explanations may be mere opinions based upon no or but few scientific facts. One is also frequently struck with the immense literature that has been produced and the great gap that still intervenes between the accumulated facts and a clear understanding of the processes which they aim to elucidate, even after more than a hundred years of experimental work, which has usually been preceded by a much longer period of speculation by the great thinkers of the past. So that while we congratulate the last few generations upon the rapid growth that has been made in scientific knowledge, there yet remain phenomena that are almost as unintelligible to-day as they were a hundred years ago—the most earnest and often tedious experimentation and observations of several generations having shed but little light on the factors and mechanism involved.

The extremely interesting fact of hibernation (called "Winterschlaf" by the Germans, "sommeil hivernal" by the French and "letargo" by the Italians) illustrates well the above point. As is well known, during this dormant state the vital processes are greatly reduced. The changes that occur are especially marked in certain mammals, since they apparently undergo a rather sudden transformation from the warm-blooded (homoiothermal) type to the cold-blooded (poikilothermal) type. In the latter state such mammals are able to endure cold, deprivation of food, confined air, effects of many drugs, and other conditions that would be fatal at other times. Naturally

such profound physiological changes, in some respects almost as striking as the latent vitality of the seeds of plants and the spores of lower organisms, has aroused the attention of a great many observers. In fact, the literature on hibernation dates back to the time of Aristotle (384–322 B.C.), though real experimental work for the purpose of understanding the nature and cause of this torpid state, commenced with Conrad Gessner¹ (1551). From that date to the present there has accumulated a vast amount of data, the bibliography of which is now very accessible, due to the extensive works of Raphael Dubois,² published in 1896, and of Osvaldo Polimanti,³ published in 1912.

As the exciting cause of so-called winter-sleep, cold has naturally received by far the greatest share of attention. A rapid survey of the subject shows that much difference of opinion has existed in regard to the manner in which cold acts and what other factors are involved. (1749) and Lacépède⁵ (1829) thought that the blood simply becomes cold when the small amount of heat produced by hibernating animals is not aided by the surrounding temperature. The cold blood then produces the changes characteristic of torpidity. Spallanzani⁶ (1787), however, considered that he had experimentally demonstrated that the cold acts on the solid tissues of the body and not on the blood. According to him the lethargy is due either to the stiffening of the muscles or to the depletion of the cerebral blood vessels. On the other hand, Alibert⁷ maintained that the cold diverts the blood from the periphery to the vessels of the brain and the resulting congestion causes torpor. But Serbelloni⁸ (1866) claims to have found the vessels of the brain nearly empty in the case of three marmots in full hibernation. Hunter⁹ (1775) and Serbelloni explained that the cold causes the animal to lose its appetite and in the absence of hunger, which is a stimulus, the animal retires.

A long list of authors, Daubenton¹⁰ (1760), Geoffroy,¹¹ Cleghorn,¹² Allemand,¹³ Carlisle¹⁴ (1805), Barkow¹⁵

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(1846) and others, have emphasized also the necessity of confined air or diminished respiration, Cleghorn and Allemand maintaining that this is the principal cause. Reeve¹⁶ (1809) said that such a condition favors wintersleep, while Bert¹⁷ (1868) first concluded that lack of oxygen and then later¹⁸ (1873) that the accumulation of CO₂ in the surrounding air might be the cause of dormancy. Mangili¹⁹ (1807), however, denied that vitiated air has anything to do with this torpid state and Dubois²⁰ (1896) says that confined air is not necessary, for animals hibernate perfectly in well-ventilated places.

Marshall Hall²¹ (1832) believed that the cold caused ordinary sleep, which diminishes respiration, and less heat is produced. Lessened respiration causes the blood to lose its arterial character and hence its power to stimulate the heart. The heart, however, changes its irritability so that it does not stop. This change in the irritability of the heart, then, is the important factor in hibernation. To him winter-sleep is something entirely different from the torpor produced by cold. To Edwards²² (1824) and Legallois²³ (1824) sleep and cold are so bound up with heat production that a failure to keep up the body temperature causes torpidity to ensue.

Throughout the literature of the last one hundred years there is a strong tendency to consider hibernation as differing from ordinary daily sleep only in degree. Edwards²² (1824), Dugé²⁴ (1838), Hall²¹ (1832), Blandet²⁵ (1864), Patrizi²⁶ (1894), Dubois²⁷ (1896, 1910), Brunelli²⁸ (1902), Claparède²⁹ (1905), Allen Cleghorn³⁰ (1910) and Salmon³¹ (1910) make definite statements regarding the striking similarity between ordinary daily sleep and hibernation. Gemelli³² (1906) used the facts obtained by him from hibernating marmots, in disproving Salmon's theory of sleep. Indeed, it has been the hope of many of the students of hibernation to be able to throw some light on the process of diurnal sleep in man and other animals, by a study of what they have considered to be merely an extreme example of this physiological condition. The

discussions on sleep that appeared in the British Medical Journal in 1913 and the comprehensive treatise by Pieron³³ (1913) on the physiological problem of sleep, clearly indicate how little has been accomplished in this direction. Buffon⁴ (1749), on the other hand, thought that ordinary sleep and hibernation were something entirely different. Monti³⁴ (1905) even now believes that these two forms of sleep have entirely different physiological meanings and that hibernation in its phylogenetic study should be compared with the dormancy of lower forms, as well as with ordinary sleep.

In reply to the question asked by the French Academy of Science over a hundred years ago as to the cause of this lethargy and why it pertains to certain animals, Saissy³⁵ (1808) stated that the cause fundamentally is to be found in certain anatomical peculiarities such as the enlarged character of the heart, central blood vessels, thorax, abdomen and cutaneous nerves, and the smallness of the peripheral vessels and lungs. To these he also added as important features the liquid quality of the blood and the sweetness of the bile. The diversion of the blood from the surface towards the center of the body, as a result of the external cold, dilates the heart and blood vessels of the thorax, and this interferes with respiration. thus decreasing heat production. As a consequence the animal becomes cold and numb. Prunelle³⁶ (1811), Bar kow^{15} (1846), Serbelloni⁸ (1866) and Blandet²⁵ (1864) similarly believed in the importance of such-largely imaginary—morphological features.

Many investigators have associated hibernation with the nervous system. Claude Bernard³⁷ (1855–76) thought that the cold acts on an unusually well developed peripheral nervous system, and by slowing respiration cools the body. This is a loss of stimulus to the heart and muscles and torpor results. Reeve¹⁶ (1809) stated that cold acts on a special organization of the nervous system, which causes diminished respiration, etc.; while Quincke³⁸ (1882) interprets the facts he and others have observed,

in connection with the marmot, as indicating the existence of a heat center in the brain through whose influence on the various organs of the body, metabolism and heat regulation are so affected as to produce winter-sleep. altered respiration and circulation are secondary results. Dutto³⁹ (1896) is also inclined to believe that hibernation strictly depends upon the regulative influence of the nervous system upon metabolism and thermogenesis. further considers that the marmot has the power to emit more heat than has the rabbit, so that torpor may be based upon the difference in the power of the integuments of hibernating and non-hibernating animals to lose heat. Merzbacher⁴⁰ (1904), after reviewing much of the literature dealing particularly with the rôle of the external temperature, food and the nervous system in the production of winter-sleep, concludes that the external cold is only a secondary aid. Cold, like abstinence from food, immobility, slower respiration and lack of oxygen, simply makes it easier for the animal to cool off and remain cold, and tends to make the sleep more profound. The essential characteristic of the hibernating animal, as compared with the non-hibernating animal, according to him, is its ability to change at a rather definite period and in a comparatively short time from the homoiothermal to the poikilothermal type and again at the end of hibernation to return rather abruptly to the former condition. explanation of both of these alterations, he thinks, is probably to be found in a certain nervous mechanism in the mid-brain and medulla which is capable of influencing respiration, circulation and metabolism, and, in short, the production and loss of heat. The other changes characteristic of the lethargy are natural consequences of and adaptations to the hypothermic and hypofunctional condition.

In addition to other internal factors there is, according to Barkow¹⁵ (1846), a special susceptibility to the external cold due to a rather primitive organization of hibernating animals. Noè⁴¹ (1903) thinks that a primitive

structure of the organism is the important cause of the lethargy; but it acts as a mechanism of economy by increasing the resistance of the animal to cold, rather than to starvation, and thus prevents histolysis from reaching a dangerous point. An inefficient heat-regulating mechanism has been considered the true explanation of wintersleep by such men as Dugès²⁴ (1838), Marès⁴² (1889), and Polimanti⁴³ (1904). Simpson⁴⁴ (1911) in this laboratory has shown that the woodchuck can not be said to ever have a normal temperature in the sense that a homoiothermal animal has. Merzbacher⁴⁰ (1904) cites many cases similarly indicating the weak thermogenic organization among winter-sleepers. Recently Polimanti⁴⁵ (1914) has explained his views concerning this labile thermogenic organization. To him it is due to the fact that at some remote period all animals then existing periodically fell into lethargy. With evolutionary development most mammals and all birds lost this ability. Hibernating animals, however, are still able to return to this cold-blooded type when the heat-producing reflexes fail, which they are apt to do when the cold becomes extreme. Marès⁴⁶ (1913) holds fundamentally this same view—a view he advanced in 1889. He says that the cause of hibernation is in the organism itself. He regards the facts presented by Pembrev⁴⁷ and Babák⁴⁸ and others concerning the poor heat-regulating mechanism of the newborn in man and other animals, as well as those by Merzbacher⁴⁹ on the return of the nervous system to a more segmental type during winter-sleep, as strong evidence in favor of the theory, and as indicating that hibernating animals merely revert to a more primitive type in which there is no specific sensibility to the outer cold, i. e., in which no specific heat-regulating reflexes are called forth by the external temperature. He further thinks that since the weakness is in the nervous system, it ought to be possible to bring about some of the conditions of torpor by means of hypnotic suggestions. He and Hellich⁵⁰ (1889) succeeded by this means in getting a fall of

2.5° C. in the body temperature of a hysterical woman. Others have gone much farther in this regard. Liébeault⁵¹ (1866) and Forel⁵⁹ (1877), especially the latter, consider hibernation similar in nature to hypnotic sleep. To Marès, however, the initial cause of winter-sleep is the ability of the nervous system to loose its specific sensitiveness to the external cold. This sensitiveness, he thinks, does not belong to the fundamental properties of the nervous system, since it is not found in the young undeveloped animal. It is a property acquired slowly ontogenetically just as it was slowly acquired phylogenetically by the two highest classes of animals. A similarity between the hibernating and fetal states was noted long ago by Pallas⁵³ (1778), Prunelle³⁶ (1811), Tiedermann⁵⁴ (1815) and Edwards²² (1824). Tiedermann claimed that in both states there is merely a vegetative existence, hardly any appreciable difference between the appearance of the venous and arterial blood, much serum and little clot when the blood coagulates, a low body temperature, an enlarged thymus (he included the hibernating gland as part of the thymus) containing a fluid, and a secretion of bile. He therefore considered winter-sleep as a periodic return to a fetal state. Pembrey and Hale White⁵⁵ (1896) regard the evolution of hibernation, not as the acquisition of a new power, but as a retention of one already present, as is evident from the condition of young mammals and birds in whom the heat-regulating power is inefficient.

Many observers have questioned the value of cold as a factor in the production of this dormant state. Quincke³⁸ (1882) thought that rest and an appropriate temperature generally, though not always, cause torpor, and yet he said that there seems to be some relationship between degrees of lethargy and external temperature. Blandet²⁵ (1864) considered that winter was only occasionally, if at all, the cause; while Horvath⁵⁶ (1872–81), with whom Bunge⁵⁷ (1901) seems to agree, said that hibernation is not sleep at all and that winter has nothing to do with it.

Hahn⁵⁸ (1914) concludes that the torpid condition is not dependent upon cold weather, although his thirteen-lined ground squirrel usually hibernated with each cold spell and woke up with the return of warm weather. Experimentally it was early shown that cold will not induce typical lethargy. Thus Buffon⁴ (1749) in the case of the hedgehog, Daubenton⁵⁹ in the hamster, Hunter⁹ (1775) in the dormouse, Mangili¹⁹ (1807) and Bossi⁶⁰ in the marmot, Horvath⁵⁶ in the spermophile and hedgehog and Marès⁴² (1892) in the spermophile, have failed to induce true hibernation by exposure of the animal to low temperatures. Saissy³⁵ (1808) is supposed to have produced winter-sleep by continued cold and confined air; but like some other reported cases of artificially produced torpor, it is not clear that the experimentally produced state was the same as true hibernation. Sacc⁶¹ (1858) after eight vears of observation on the marmot could see no relationship between the condition of the atmosphere and winter-Mills⁶² (1892) found that while bats could be worked like a machine by varying the temperature, marmots, on the contrary, showed a surprising indifference to the surrounding temperature. Berthold⁶³ claims that dormice became dormant in a room kept warm (16° C.) all winter, though torpidity was delayed two months. Merzbacher⁴⁰. (1904) mentions similar experiences of his own with a bat, as well as several other comparable cases. Mangili¹⁹ (1818) saw a dormouse fall into lethargy in the month of June and not wake up till the middle of July. Forel⁵² (1887) records that two dormice which remained awake and active all winter, became torpid in May and remained in this condition till August in spite of the great heat. Marès⁴² (1892) found that some spermophiles and hamsters may hibernate in September at 16° C, while others remain awake all winter although the thermometer falls below zero. Hence he concluded that cold does not cause winter-sleep. Valentine⁶⁴ (1857). Horvath⁵⁶ (1881) and Quincke³⁸ (1882) have observed marmots become dormant during the summer. Hence Pembrey⁶⁵ (1898), while recognizing that want of food and cold seem to be the most important factors in hibernation, says that some other condition yet unknown is necessary to explain such lethargy during the summer.

As a result of the uncertain action of cold, certain other external conditions have been considered the real exciting cause of hibernation. The food factor was emphasized by Mangili¹⁹ (1807), who believed that neither cold nor vitiated air has anything to do with the production of this torpid state. He thought fasting was necessary because, of several animals under the same external conditions, those animals that were fed did not become dormant, while the non-fed ones did. Marshall Hall²¹ (1832) stated that the lack of food predisposes the animal to torpor by rendering it more susceptible to cold. (1858) concluded that, while he could see no relationship between the atmosphere and torpidity, he could see some connection between the fatness of the animal and the length and profoundness of winter-sleep. He, therefore, concluded that obesity, in connection with fatigue, is the cause of hibernation. Claparède²⁹ (1905) and Forel⁵² (1887) think that the amount of fat may be an important factor, while Beretta⁶⁶ (1902) opposes this idea. son⁶⁷ (1912) finds that feeding woodchucks greatly interferes with winter-sleep, at least in captivity. Albini68 (1901) in case of the marmot, and Reeve¹⁶ (1809) in connection with dormice and hedgehogs, also confirm the observation of Mangili on the rôle of food in preventing hibernation. Yet it appears that these animals (marmots) may go into winter sleep while plenty of food is Thus Mills⁶² (1892) found that during the winter of 1890-91 a marmot hibernated in a cage provided at all times with plenty of food; but during the two following winters two other marmots, kept in the same room and in the same cage under similar conditions, did not hibernate at all, though the temperature got low enough to freeze the water in the cage. It is also a common observation that some of these animals naturally retire while food is plentiful. Allen Cleghorn³⁰ (1910) questions the lack of food as a factor in producing lethargy because spermophiles and marmots hide away for winter when their food supply is at its best. In British Columbia he finds that these animals retire a month earlier in the lowland than at the timber line because, he thinks, in the latter region they have not had time to acquire enough fat, since at the timber line they come out of hibernation later in the spring. Thus it is not clear exactly what part food plays in the production of this dormant state.

Treviranus⁶⁹ (1802) said that the cause of torpidity during winter lies in the ability to live with all the vital processes at a minimum. This is an acquired character resulting from the habit of sleeping during winter, as is evident, he thought, from the fact that it is lost in marmots kept in captivity. The earlier opinion of Barton⁷⁰ (1799) was that it is an accidental circumstance and not a specific character. The general idea, however, that some sort of instinct, in connection with other factors, is involved, was held by Reeve¹⁶ (1803), Barkow¹⁵ (1846), Claparède²⁹ (1905) and others. Desjardine⁷¹ thought that the need for sleep in rodents is as great as the necessity of migration in birds. Blandet²⁵ (1864) described winter-sleep as a relic—an echo from remote periods when this phenomenon was general, having developed as a result of winters so severe that unless this conserving process was resorted to, the animals would have perished. Hibernation is thus, according to this author, the effect of habit and annual periodicity. It still persists in certain animals, but will soon become extinct. Brunelli²⁸ (1902) believes that this tendency is the result of a long period of evolution favored by the nature of the burrow, etc., where hibernation takes place. But according to Albini⁶⁸ (1894) the factors aiding this evolution are not remoteness or other conditions of the burrow, but the immobility of the animal. Carlier⁷² more recently (1911) classifies hibernation with estivation (summer-sleep) and migration. Winter-sleep in mammals like the instinct of migration in birds, he thinks, may have developed in remote ages, the prime cause being want of food, and not cold.

Dubois⁷³ (1895) has developed a carbonic auto-narcosis theory according to which hibernation is due to the accumulation of CO₂ in the blood and tissues of the animal. This excess of CO₂ is supposed to cause a form of narcosis as seen in the torpid condition of the hibernating When the CO₂ reaches a certain concentration the respiratory center is excited, respiration accelerated, and the muscles become hyper-irritable. These culminating results are responsible for the awakening from dor-The author claims that he can induce typical hibernating sleep by causing the active marmot to breathe a mixture of air (42 per cent), CO₂ (45 per cent) and oxygen (12 per cent). Torpid marmots remain dormant if supplied with this mixture. By increasing the proportion of CO₂ respiration is accelerated, and if the supplying of CO, is continued the hibernating marmot wakes up. The CO₂ is supposed to act principally on a nervous center for sleep situated in the mid-brain, since marmots deprived of cerebral hemispheres are able to sleep and wake up; but with only the medulla intact they are unable to awake. Further, Dubois⁷⁴ (1894) found that CO₂ actually accumulates in the blood during hibernation in the marmot and decreases again when the animal wakes Such an increase in the CO₂ content of the blood during hibernation has just been observed in this laboratory in case of the woodchuck (Marmota monax). 75

Upon sufficiently good authority⁷⁶ to receive the serious consideration of such an author as Max Verworn,⁷⁷ certain ascetics of India, known as fakirs, are able to voluntarily go into a condition of almost suspended animation not unlike hibernation in some respects. While in this condition it appears that these fakirs may be buried three or four feet in the ground for days, or may be inclosed for six weeks without food and with but little air in a tight box which in turn is sealed up in some dark inner room.

When disinterred the body is cold and stiff with no signs of any pulse, and apparently lifeless; but it revives with no bad after-effects upon the application of warm water to the head and after being manipulated for a quarter of an hour. Dubois emphasizes the fact that in order to induce this state of trance, the fakirs make it a point to breathe as little as possible. This and much other indirect evidence is brought forward by this author in support of his carbonic auto-narcosis theory of hibernation.

Mosso⁷⁸ (1899) holds just the opposite view. He thinks that winter-sleep is due to a condition of acapnia, or lack of CO₂ in the system.

It is not strange that in this age of ductless glands and internal secretions some theory should be brought forward that would involve the ductless glands. In 1905 Salmon⁷⁹ advanced the view that the pituitary body (hypophysis cerebri) is a center for sleep and produces an internal secretion which by virtue of some vasomotor or autotoxic power acts on the nervous system and thus produces normal sleep. His view has been further elaborated in later publications⁸⁰ (1910) in which he states that hibernation may be explained upon an analogous mechanism involving especially the so-called hibernating gland -a structure which has lately received renewed attention by physiologists. Salmon seems to favor the old idea that a depletion of the cerebral blood vessels offers the best explanation of the lethargy characteristic of the hi-The rôle of the hibernating gland, howbernating state. ever, is very uncertain. This structure is now generally regarded as reserved food. Vignes⁸¹ (1913), however, considers it probable that it plays some important physiological rôle, particularly in hibernation, since its extirpation in the white rat, where the operation is attended with little difficulty, is nearly always fatal. finds that this structure modifies the action of certain toxic substances such as adrenalin, chloroform, tetanus toxin and cobra venom, retarding the action of some and accelerating that of others. He further maintains that this gland contains lipase, and while it does not convert starch to sugar, its extirpation diminishes the amyloptic power of the serum. It also has an antitryptic power. Thus he conceives that it might serve as an economizer of proteins by insuring the utilization of reserve carbohydrate and fats during the long period of winter-sleep.

Salmon's view on the rôle of the hypophysis cerebri in the production of sleep was soon criticized by Gemelli³² (1906), who argued that if this hypothesis were correct, the pituitary body would show signs of increased activity during hibernation, since, as has already been stated, hibernation is considered by many to differ from ordinary diurnal sleep only in degree and duration. But on the contrary, he found that the cyanophil cells of this gland in the marmot decreased during winter-sleep and that they increased again simultaneously with the appearance of numerous karyokinetic figures after the animal wakes up in the spring. Gemelli interpreted his findings as indicating that the anterior lobe of this organ cooperates with other ductless glands in neutralizing toxins which are produced in increased quantity when the animal becomes active, and hence is not to be regarded as a center of sleep. A later contribution to the relationship between the pituitary body and hibernation is by Cushing and Goetsch⁸² (1913). As a result of observations on the hypophysis of the woodchuck, in which they confirm in general the findings of Gemelli on the decrease in size and histological changes during winter-sleep, these authors suggest that hibernation may be ascribed to a period of physiological inactivity, possibly of the entire ductless gland series, but certainly more especially of the pituitary gland, because during the dormant period this structure diminishes in size and shows profound histological changes and because deprivation of this gland in the human subject and in experimental animals causes a train of symptoms comparable to those of hibernation. Mann⁸³ (1916), however, found demonstrable changes in the pituitary body and other ductless glands of a large number of ground-squirrels (Citellus tridecemlineatus) to be absent or so inconstant, especially at the critical period—at the onset of hibernation—that the assumption of any theory ascribing the phenomenon of hibernation to a lack of function of all or any one of the ductless glands is not justified.

From this general summary it will be seen that great diversity of opinion prevails regarding the immediate cause of this extremely interesting condition, and of the sudden transformation from the homoiothermal to the poikilothermal state (and vice versa) so characteristic of hibernating mammals. It is not the author's object, however, to discuss the relative merits of the various Suffice it to say that all of them are based upon insufficient data. To say which of the various conditions associated or occurring simultaneously with winter-sleep are concerned with the production of the lethargy and which are the results of this or some other condition, is extremely difficult. Until certain causal relations are definitely established between the factors concerned, many of these theories are of very little value except as a stimulus to further research. It is thus very evident that we are far from having any adequate explanation of the mechanism of this phenomenon, to say nothing of how it was established as a more or less variable character in certain animals.

If hibernation of mammals is only an extreme form of ordinary diurnal sleep of man and other animals, it is especially to be hoped that this subject will continue to be investigated by more modern and adequate means, for no entirely satisfactory theory has yet been advanced to explain the physiological cause of ordinary sleep. Since winter-sleep may also be attended with total abstinence from food and drink for many months, the facts derived from a study of the various conditions associated with this dormant period are of interest also in connection with the subject of inanition in particular and metabolism in general, as is plainly indicated by the frequent reference

to and comparison with the observations on hibernating animals found in the literature on inanition.

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